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# PRELIMINARY NOTE ON THE DISTRIBUTION OF THE TIGER BEETLES (CICINDELA) AND ITS RELATION TO PLANT SUCCESSION.

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The adult beetles are graceful, predatory, swift-flying insects whose definite distribution and great variability have long been matters of comment. The larvæ have been found to be more circumscribed and definite in their distribution than the adults. Our attention has accordingly been turned to the behavior of the larvæ and of the adults at the time of egg laying for a possible explanation.

The egg laying habits are simple. The last four segments of the abdomen are used as an ovipositor. Two pairs of the appendages of these segments serve as digging organs with which small vertical, well-like holes from 7 to 10 mm. deep are made in the soil. A single egg is deposited in a hole and the hole is left uncovered. The tenth segment of the abdomen and one pair of appendages of the ninth segment are covered with hairs which are probably associated with organs sensitive to the varying degrees of soil moisture and the size of soil particles. The females try the soil before depositing eggs. They make many holes, but lay in only a part of them, and frequently discard them before the usual depth is attained.

The larvæ almost always remain in the spot where the eggs were laid. Upon hatching each larva constructs a burrow in the place of the ovipositor-hole and reconstructs and enlarges the burrow after each moult. If a larva migrates, it almost always selects the same kind of place for digging a new hole as that in which the eggs were laid.

So much for the general aspects of the life habits. Let us now turn to some examples of distribution and behavior during the egg-laying time.

The larvæ of *Cicindela purpurea limbalis* are found on steep

clay banks.<sup>1</sup> The range of the adults is far wider. To determine the cause of this distribution, adults were placed in cages containing soil of several kinds. Each kind was so arranged into steep and level parts that about one square foot of each type was exposed. The adults placed in the cages were taken when the species was copulating freely.

The following table shows the number of larvæ which appeared in the case of three lots of *C. purpurea limbalis*.

Soil.	Humus.		Clay and Humus.		Clay.		lean Sand.		Sand and Humus.	
<i>S</i> = Steep, <i>L</i> = Level.	<i>S</i>	<i>L</i>	<i>S</i>	<i>L</i>	<i>S</i>	<i>L</i>	<i>S</i>	<i>L</i>	<i>S</i>	<i>L</i>
I. No. of Larvæ.	0	0	0	0	9	0	0	0	0	0
II. No. of Larvæ.	0	0	0	0	12	1	0	0	0	0
III. No. of Larvæ.	0	0	1	0	24	10	0	0	0	0

Other pairs taken in coitus were placed in cages containing sand only and level clay only. No larvæ appeared in either case. Females placed in cages containing rough steep clay, deposited eggs. Similar experiments have been carried out on several other species and it becomes apparent, therefrom, that the local distribution is determined by the egg-laying instincts. Since the animals cannot and do not continuously remain far from the breeding place, the breeding place becomes the true index of their habitat. Their local distribution being determined by egg-laying instincts, in other words by the life needs, and housekeeping habits of the animals, it may be called "ecological distribution" from Haeckel's<sup>2</sup> definition of that term, and the etymology of the word.

Habitat selection in correlation with geological factors such as erosion and deposition, and with the succession of plant formations and societies forms one of the great factors of dispersal, isolation, etc.

<sup>1</sup> The nomenclature used in this paper is to be found in Horn's "Systematischer Index der Cicindeliden," *Deut. Ent. Zeit.*, Feb., 1905, Supplement. *C. scutellaris* Say, however, stands in that publication as *obscura* Say aber. *Lecontei* Hald., the corresponding change having been made by the same author in a later publication.

<sup>2</sup> Ecology is the science of the domestic side of organic life, of the life needs of organisms and their relation to other organisms with which they live. "Wonders of Life," 1905.

The relation of the distribution of *Cicindela* to the succession of plant societies has been especially studied in the vicinity of Chicago. The area which affords the basis of this study is to be found at the south end of Lake Michigan. Conditions here since glacial times have led to the deposition of large areas of sand, which in the eastern portion of the field of deposit, is stretched over an area of several miles wide. At the point where most of the studies have been made there is a series of ridges which were originally thrown up under water and later added to by aerial deposition. These ridges are separated by long depressions, most of which contain water. The structures are accordingly arranged in a horizontal series, the oldest being, of course, furthest from the lake, and differing from the younger only in age, and in being a little less exposed.

A definite succession of plant societies has been worked out by the plant ecologists (Cowles and Clements) and this succession is due largely to the conditions necessary for the germination of the seeds and growth of the seedlings of the different plants. In forest development, before the climax stage is reached, the seeds of the trees comprising a given stage do not germinate and their seedlings do not develop in the shade of the forest then present. Each stage accordingly prepares for another and more mesophytic type. The trees of the climax stage of eastern North America, the beech and the maple, produce seeds that will germinate in that forest's own shade. Accordingly the beech and maple will last indefinitely.

Not all of the conditions herein described occur in the horizontal series at any one point, but all are to be found within sandy areas near Chicago.

Let us start with the strip next to the water's edge, the very youngest deposit. It is frequented by the adults of *C. cuprascens* and *hirticollis*. The larvæ of the latter are sometimes found here, but more frequently a little further back on the low, wet places on the beach. Other ridges are seen to be formed beneath the water and this margin is accordingly potentially the first depression.

On the lakeward side of the first ridge, among the young cottonwoods, we find the larvæ of *lepida*, the white tiger beetle. On the leeward side where bunch-grass has come in and the cotton-

woods are old with occasional seedlings of gray pine intermixed, we find the larvæ of *C. lepida* displaced by those of *C. formosa* var. *generosa*, which reach their dominance among the young pines.

Coming in on the ridges with the pine are the larvæ of *C. scutellaris*. In our horizontal series this species is to be found further from the lake than any others yet mentioned. As new ridges are thrown up outside of a given one and as it becomes older, the differences between the lakeward and the landward exposure quickly disappear.

Let us turn our attention for a moment to depressions. We have noted that *C. hirticollis* occupies a station on the white sand of the beach. In addition to occurring occasionally in the wet situations just mentioned, the larvæ are found in any of the fresh natural depressions that are deep enough to be continually moist at, or near the bottom. Such depressions sometimes occur on our lake shore, behind a first line of small dunes. As a depression becomes older and the sand becomes somewhat darkened by the decay of the reed, *Juncus balticus*, the larvæ of *C. hirticollis* give way to those of *C. repanda* which occur a little higher up than the former, on the sloping sides of the depressions. As the *Juncus* becomes thicker and a few other plants come in, the larvæ of *C. repanda* become a little less numerous. We have been able to follow this process in an artificial depression. Finally the vegetation becomes so dense as to drive out the larvæ of *C. repanda* entirely. They are succeeded by the larvæ of *C. tranquebarica* which occur still higher up the side of the depression. This stage is coincident with the development of young gray pines on the ridges.

Shrubs of various sorts appear on the depression margins at this stage and gradually increase in numbers. The first are the willows and the shrubby cinquefoils. These are succeeded by the button bush and swamp white oaks which make the depression margin too shaded for the larvæ of *C. tranquebarica* and the tiger beetle succession of the depression margins is at an end. This stage of the depressions corresponds to the establishment of the black oak, which succeeds the pine, on the ridges.

Returning to *C. scutellaris* at this stage, we find it still, in the

open places of the black oak ridges. These oaks are destined not to remain and are crowded out by the coming in of the white oaks. For an immense period after this, the habitats of *C. scutellaris* become more and more narrowed. Long before the next tree, the red oak, makes its appearance, *C. scutellaris* has been crowded out. Many centuries must pass between the coming in of the white oak and the establishment of the red during much of which time the *Cicindelas* are entirely absent. With the establishment of the red oak, conditions are ready for the next tree, the shag-bark hickory, and with it comes *C. sexguttata*. This species appears to reach its dominance in the early stages of the white oak-red oak-hickory forest, and to be crowded into its margins with the development of further mesophytism. It continues in the roads, clearings, fired places, and paths of cyclones in this forest for a long period. Individuals are sometimes to be found in the dense parts about a fallen tree. This type of forest is, however, destined to disappear and its disappearance is heralded by the coming in of the seedlings of the beech and the maple. With their appearance *C. sexguttata* becomes rare in the forest proper.

This species does not deposit eggs in pure humus, but makes use of little irregularities in clay or sand, which, contains a little humus and which is shaded slightly, such conditions as are afforded by falling trees and the erosion of hill sides by small brooks. It prefers a few loose leaves and will lay eggs under them in preference to other places when they are present. It does not, however, appear to like very shady conditions. Several days spent in the beech and maple forest has failed to reveal the presence of one of these insects although they were present in open and partially cleared places a short distance away where the forest has not become so mesophytic.

The beech and maple forest is very shady and has a floor of decaying leaves about one inch deep and several inches of very mouldy humus below these, so that there is no place in the forest proper where *C. sexguttata* can deposit eggs. It is driven out by the development of these conditions.

The white oak-red oak-hickory forest is now distributed over much of the eastern half of northern North America, but the climate in which the beech and maple will develop extends west-

ward only to the Mississippi and Illinois rivers. Dr. Cowles, whose work is still unpublished, has studied the forest of the eastern United States and has come to the conclusion that with the base leveling of the eastern plateau the beech and maple forest would, man eliminated, succeed the less mesophytic types and come to completely cover the territory extending to the western limit of its climatic range. This forest would then come to occupy the entire territory east of the Mississippi and Illinois rivers. This means the driving out of *C. sexguttata* which is now abundant in the forest of this region. Not at once, to be sure, but irregularly and gradually, first giving irregular and finally discontinuous distribution with a constant narrowing of the range of the isolated habitats. For immense ages habitats would no doubt continue to exist, but since the differences between the different elevations and brook and river margins on the one hand and the climax forest on the other become less and less as the development of the climax stage proceeds, the chances for the maintenance of habitats of *C. sexguttata* indefinitely, seem small.

The general effect of the development of these conditions on the distribution, would be as follows: *C. sexguttata* would be left only in that portion of its present range, west of the climatic conditions suitable for the development of the beech and maple forest, with possible remnants in the eastern plateau which might by a process of isolation, be caused to take on new habitats and new characters.

The general principles here set forth apply to the *Cicindelas* associated with the development of rivers and the erosion of uplands. Observations now under way go to show that they apply to the fauna in general. Strikingly different faunas are to be found in the different forest stages herein mentioned. Plant succession is then a factor which we cannot afford to neglect in considering distribution and evolution.

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